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Population dynamics of the Red squirrel in Bavaria

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Abstract

Describes the population dynamics of the red squirrel *(Sciurus vulgaris)* in Bavaria since the early 1970s. A decline in the population of squirrels was found between 1970 and 1980, while recently an increase was recorded. The decline can be attributed to reproductive waves caused by mast years of coniferous trees. The recent increase can be explained by general forest decline, since damage to trees desynchronizes seed production and squirrels are provided with a constant food resource over a number of years.

Weather conditions were found to be unimportant for the population dynamics of squirrels. For the beech marten *(Martes foina)*, however, a negative correlation could be demonstrated between number of squirrels and this predator at one study site.

Introduction

Compared to birds the available data on long-term fluctuations of medium-sized mammals are very rare. This is due to the difficulties to trap and count these animals within a reasonable period of time. Even for diurnal species like the red squirrel *(Sciurus vulgaris)* only a limited amount of information is available. Long-term series are badly needed to document the full range of patterns in the population dynamics of mammals. In game biology there is a long tradition to use hunting bags or other indirect measures to document fluctuations in game animals (for a recent example see Potts et al. 1984). We followed this line of investigations and present indirect density indices to describe the dynamics of the red squirrel in Bavaria. We concentrate on the following questions:

1. Are there any long-term trends in the population of squirrels in Bavaria? In two reports we suggested that there was a decline in numbers of squirrels since the early 1970s (Brandl 1983; Reichholf 1983).
2. Is the dynamics of the squirrel populations similar in different regions of Bavaria?
3. The main food of the red squirrel is the seeds of coniferous trees (Wiltafsky 1978). Many studies have shown that the populations of squirrels follow seed production (Formosov 1933; Pulliainen 1984; Reichholf 1974). Is this pattern also evident within our sets of data?
4. The red squirrel is the prey of several predators such as the pine and beech marten (*Martes martes, M. foina;* Stubbe 1988). Do these species have some influence on the populations of the red squirrel?

Material and methods

In the following we name each data set by its geographical location (see Fig. 1):

1. Pressath: This data set consists of specimens delivered to a taxidermist between September and March from 1965/66 onwards to 1982/83 with a gap between 1967/68 and 1972/73 (550 individuals; Brandl 1983). The working period of the taxidermist was not constant over the years. We used the

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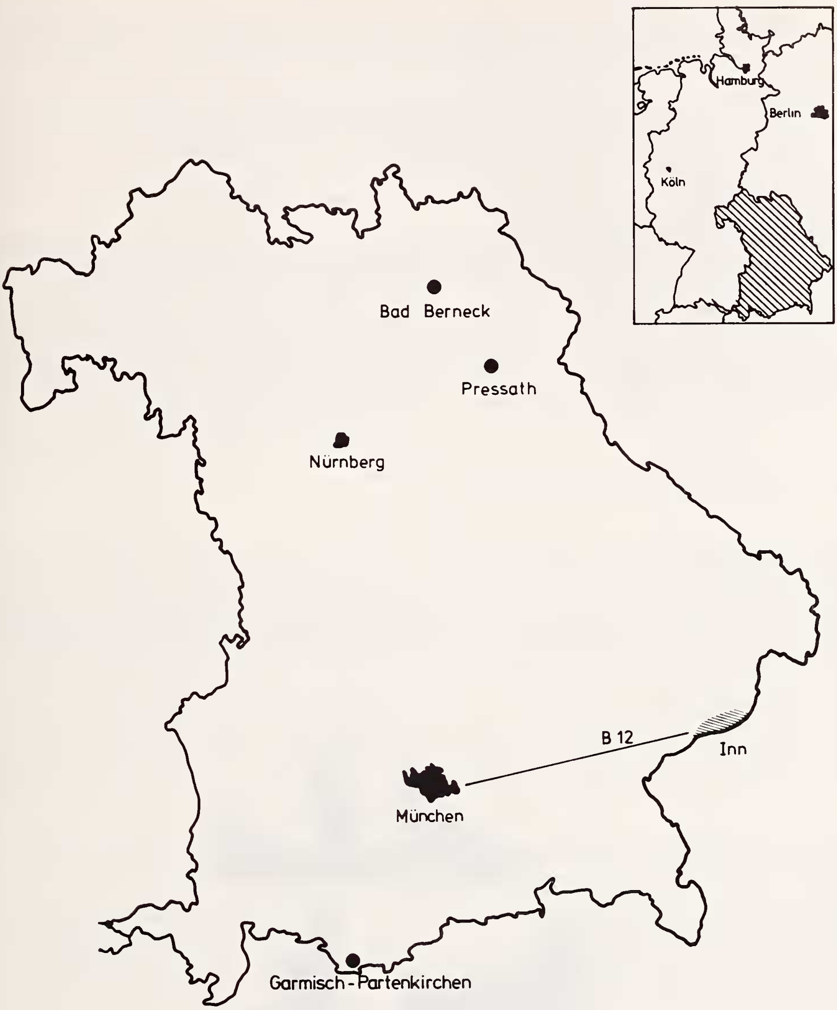

Fig. 1. Geographical location of the investigated areas in Bavaria

number of mammals and birds to standardize red squirrel data and calculated percentages of red squirrels delivered to the taxidermist.

Around Pressath the dominating types of vegetation are spruce forests *(Picea abies)* and at poorer sites pine forests *(Pinus sylvestris)*. Altitudes range from about 400 to 600 m NN.

2. Bad Berneck: Similar to Pressath these data are specimens delivered to a taxidermist between 1970 and 1988 (922 individuals). This taxidermist worked over the entire year. We standardized the data because the overall working effort appeared to vary from year to year. The number of delivered birds was used as an independent measure of the working effort. Numbers of red squirrels are expressed in individuals delivered per 100 birds.

   Bad Berneck is situated within the Fichtelgebirge. Spruce forests are the dominating type of vegetation, and the altitudes range from 500 to 1000 m. At higher altitudes winters may be quite severe.

   For this area we have also data about weather, seed production of the spruce and dynamics of one potential predator.

   a. Monthly information of rainfall and temperature was available for Bayreuth, only 10 km from Bad Berneck.
   b. The forest authorities estimate the seed production in four categories: "Vollmast" = very high

seed production, "Halbmast" = good seed production, "Sprengmast" = low seed production and no seed production. We ranked each year on this scale from 0 to 3 and allowed for intermediate values according to information of the forest authorities (available years 1971 to 1988).

c. The number of martens delivered to the taxidermist (pine and beech marten) may be used as an indicator of the predator density. The pine marten is rather uncommon in the area around Bad Berneck, so we concentrate on the beech marten. Data were standardized similar to those for squirrel numbers.

3. Inn: These data are from squirrel sightings made during standard excursions between 1971 and 1982 (153 records; Reichholf 1983).
4. B 12: Road kills are often good indicators of the population dynamics of medium-sized mammals. The B 12 data sets are the sums of road kills during a year along the federal highway B 12 between Munich and Bad Füssing (89 individuals; Reichholf 1983; 1976–1988). The killed martens were also counted along the same route.
5. Garmisch-Partenkirchen: Data are from squirrel sightings along three transects (1979 to 1988; 195 records), situated at the lower mountain forests about 800 to 900 m NN and were sampled twice each month. The dominating tree species is the spruce, but deciduous species of trees are also present. Winters may be severe with snow cover between November to April.

Results

Phenology

The seasonal distribution of data (Inn, B 12, Garmisch-Partenkirchen) is plotted in Fig. 2. The phenological patterns are similar for Inn and Garmisch-Partenkirchen ($r = 0.55$; $P < 0.05$; one-tailed). No road kills were found during January and December in contrast to the data based on squirrel sightings. All three plots showed a minimum during July.

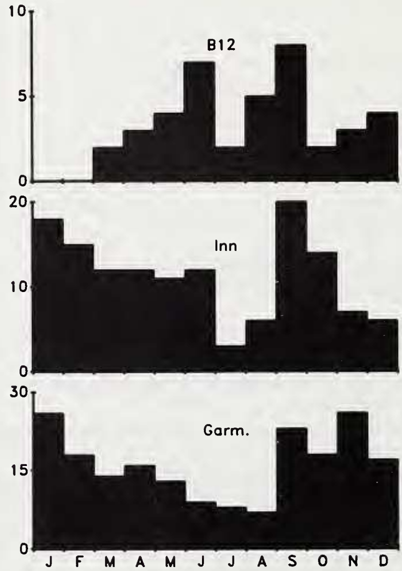

Fig. 2. Seasonal distribution of road kills (B 12) and sighting records (Inn, Garm. = Garmisch-Partenkirchen) of the red squirrel, given as the sum of sightings or road kills recorded within each month

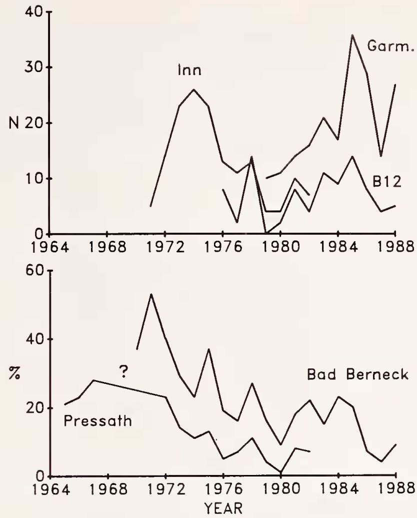

Fig. 3. Population fluctuations of the red squirrel in different areas of Bavaria. For the areas Inn, B 12 and Garmisch-Partenkirchen (Garm.) the sum of all sightings or road kills within each year is given. The data from Bad Berneck and Pressath are relative indices calculated as percentages of squirrels delivered per all animals (Pressath) or squirrels delivered per 100 birds (Bad Berneck; see Material and methods)

Population dynamics

In Fig. 3 all data sets are plotted across the years studied. The data from northern Bavaria (Bad Berneck and Pressath) show a clear decline in the squirrel populations. This decline is also apparent within the Inn data, but with an obvious peak in 1974. Since 1980 there seems to be a slight increase of squirrel populations, evident in all data sets covering this period. Furthermore, the plots show a rough concordance in minor peaks (e.g. 1975, 1978, 1983, 1985). Table 1 presents the correlation coefficients between sampling areas: all correlation coefficients are positive and six from ten are significant.

Table 1. **Matrix of pairwise correlation coefficients (upper half of the matrix) between the squirrel density indices of Fig. 3**

Each coefficient measures the similarity in the population dynamics of squirrels between a particular pair of geographical locations, considering only the years with data for both areas. The lower half of the matrix gives the significance levels of the correlation coefficients (one-tailed)

	1	2	3	4	5
1 Inn	—	0.770	0.727	0.201	0.580
2 B 12	0.021	—	0.732	0.483	0.738
3 Garmisch-P.	0.137	0.008	—	0.005	0.766
4 Bad Berneck	0.265	0.047	0.495	—	0.923
5 Pressath	0.030	0.029	0.117	0.000	—

Squirrels and predators

We concentrated on the data from Bad Berneck, because this is the longest time series. In Fig. 4A we removed the negative trend apparent in Fig. 3 by linear regression. Runs with several transformations produced identical results. Firstly, some very prominent peaks are evident by the residuals, and secondly, there is a depression in squirrel densities between 1976 and 1980. This depression within the squirrel data seems to correlate with a maximum in the population index of the beech marten (Fig. 4B). A stepwise multiple regression was performed with the squirrel data as dependent variable and years and predator density index as independent variables. The sequence of variables entering the regression was 1. year and 2. predator with a significant negative regression coefficient (see also Table 2). Fig. 5A plots the residuals from a simple regression of squirrels to years (data in Fig. 4A) against the marten index (Fig. 4B): the negative correlation between squirrels and the beech marten is evident.

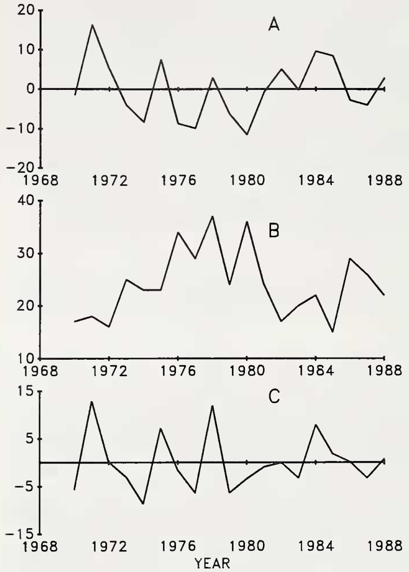

Fig. 4. A: Residuals of the red squirrel density after removing the negative trend over the years investigated. B: Dynamics of the beech marten in the same area, given as number of martens delivered per 100 birds (see Material and methods). C: Residuals of the red squirrel density after removing the trend over the years examined and the influence of the marten (all data from Bad Berneck, Fichtelgebirge)

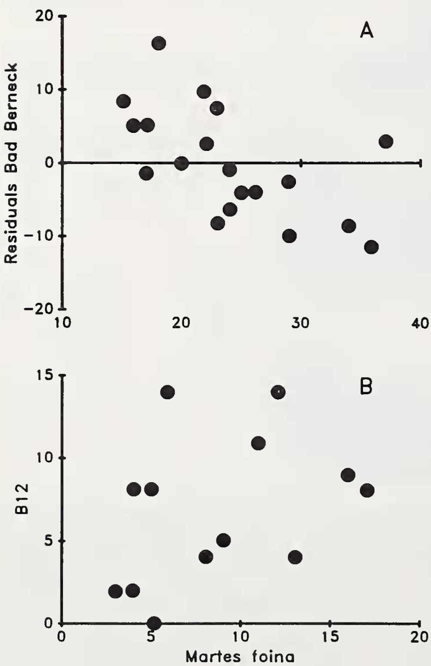

Fig. 5. A: Scatter plot of the red squirrel (after removing the negative trend over the years examined) and the populations of the beech marten (see Fig. 4 A, B; area: Bad Berneck). B: Scatter plot of road kills of squirrels and beech marten along the highway B 12

Table 2. **Stepwise multiple regression with red squirrel index from Bad Berneck as dependent variable and year, marten population and mast index of the spruce in the previous year as independent variables**

A: sequence of variables entering the regression

Step	Variable	R^2	P
1	year	0.56	< 0.001
2	marten	0.72	< 0.001
3	mast index	0.78	< 0.001

B: regression equation after step 3

Variable	Slope	Stand.slope	P
Year	−1.532	−0.78	< 0.001
Marten	−0.533	−0.35	0.02
Mast index	3.21	0.25	0.08[1]
Constant	3065		

[1] note that P is two-tailed in Table 2; in the text we used a one-tailed probability.

In Fig. 5B a scattergram was also plotted for the road kills of red squirrel and beech marten along the B 12. Contrary to the area around Bad Berneck we found no negative correlation between predator and prey (r = 0.37; P > 0.2; two-tailed).

Squirrels, food and weather

For the data set from Bad Berneck information on seed yield of spruce was available (Fig. 6B). The residuals from the multiple regression after step two in Table 2 are also shown. Seed index and residuals are significantly correlated with a time lag of one year (r = 0.48; p = 0.04; one-tailed; note that degrees of freedom have to account for the number of variables used to calculate the residuals). Table 2 shows the stepwise multiple regression of squirrel population index and the independent variables 1) year, 2) marten population and 3) mast index (one year time lag). The mast index entered the regression during the last step.

The influence of monthly rainfall and temperature patterns on the residual (Fig. 4C) for time lags for up to two years were also tested. From 60 calculated correlation coefficients

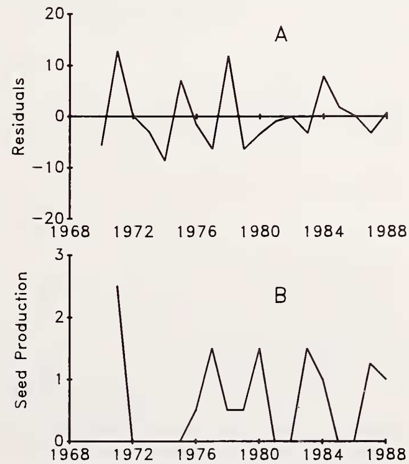

Fig. 6. A: Dynamics of the red squirrel after removing the influence of years and beech marten. B: Fluctuations in seed production of the spruce (area Bad Berneck, Fichtelgebirge)

only two were significant at the 5 % level, a result expected by chance alone. Therefore, it seems rather safe to conclude that weather conditions are unimportant for the dynamics of red squirrels.

Discussion

The seasonal distribution of the observational data and the road kills of red squirrels are quite different. During winter the red squirrel shows a reduced overall activity (Zwahlen 1975; Tonkin 1983). The reduced number of road kills are in accord with this fact. But why are so many sightings recorded during winter? The squirrel is a diurnal species with a long bimodal activity during summer, and a short unimodal pattern in winter (Tonkin 1983). In winter the peak activity is during late morning. This activity pattern may correlate with the activity of observers. Squirrels search for food during winter in the vicinity of the dreys without making longer excursions to save energy (Pulliainen 1973). That is why during transect counts squirrels are easily detected by an observer. A reduced foraging range may decrease the probability of beeing killed on the road.

Fig. 3 suggests a decline in the squirrel population in nearly all regions of Bavaria. Is this decline a natural phenomenon within the population dynamics of the squirrel, or is this decline the result of the environmental damage caused by man?

From studies in boreal regions it is well known that squirrels increase their numbers after years of a high seed yield (Formosov 1933; Pulliainen 1984). At first glance, the correlation between seed production and squirrel numbers seems to be weak in Bavaria (Table 2), but we believe that this impression is incorrect. For example Möckel (1987) described a clear increase in the red squirrel after a mast year in the West-Erzgebirge and a decline to the original density within 5 years. The availability of food after a mast year seems to improve the condition of females and thereby the probability of reproduction (Wauters and Dhondt 1989; Gurnell 1983) also under normal ambient conditions in Central Europe. The increased probability of reproduction, an increased litter size as well as better survival of young produces a population explosion in squirrels. The maximum age of red squirrels is more than 10 years, and about 1 % of individuals may reach 5 years of age or older (Wiltafsky 1978). Therefore, the explosion needs around 5 years to fade, as long as adult survival is nearly independent of seed production by trees.

1971 was one of the most important mast years of spruce within the examined time span (Reichholf 1974). As most of our data sets start in 1971 or later we are unable to document the increase in squirrel numbers: our data only show the fading of the "population wave". Furthermore, the minor mast years also produced smaller waves, and they all superposed. This scenario provides an explanation of the decline in the red squirrel since the early 1970s (Fig. 3). The negative regression coefficient of the variable year in Table 2 describes in part the lasting effects of a very prominent "population wave". The weak effect of our mast index in Table 2 is an artefact, because some of the mast-induced variation in squirrel numbers is covered by the variable year. We attribute the observed decline of the red squirrel to natural variations of the seed production of coniferous trees. The good correlations between data sets (Table 1) may be a consequence of synchronized masts across Bavaria.

Schröder et al. (1982) describe a simulation model for the capercaillie *(Tetrao urogallus)* similar to our explanation of the squirrel dynamics. Random variations in reproduction may impose long-term cycles in a species, only because adults are long-lived and independent from the factors influencing reproduction. Bad weather conditions are the cause in the capercaillie, seed production in the red squirrel. We would like to stress that the data in Fig. 3 and the simulations of Schröder et al. (1982) should act as examples for investigators studying the dynamics of long-lived species. A time series of 20 years may be too short for a complete analysis, because historical events outside the analysed time span may have lasting and confusing effects.

The high level of the squirrel index at Pressath between 1965 and 1967 is inconsistent with the view that the dynamics of the squirrel is mainly influenced by seed production. Möckel's (1987) data indicate a very low density during that period. Consequently, one may suggest that the population density of the red squirrel dropped below the level of the late 1960s after an intermediate increase induced by spruce mast in 1971. Note that we have no data for the period around 1971 for Pressath (question mark in Fig. 3).

Perhaps some people would invoke forest decline as a factor, which may negatively influence forst animals. Damage of forests is frequent in northern Bavaria (Schulze 1989). Forest decline has been prominent since the late 1970s, but the squirrel populations have increased since 1980 (see Fig. 3; Garmisch-Partenkirchen and B 12). Furthermore, forest decline may have a positive effect on species depending on seeds. The synchronized production of seeds is reduced by the damage to trees. Every year some trees produce seeds and the food supply may be more constant compared to periods with synchronized, but unpredictable seed production. Around Garmisch-Partenkirchen nests of the crossbill *(Loxia curvirostra)* were found nearly each year in the late 1980s, whereas in the 1970s broods were only observed during mast years (Bezzel unpubl.).

In the Fichtelgebirge the beech marten is negatively correlated to squirrel density (Fig. 5A). This suggests that within certain circumstances predators have some influence on prey species (note that the B 12 data did not show such a correlation!). Squirrels are only an alternative prey of the beech marten and the densitiy of the marten is regulated by different factors: the population dynamics of the squirrel has no effect on marten populations. Pulliainen (1984) found no increase in the pine marten after an increase in squirrels. In turn, an increase in predator populations may increase predation pressure on alternative prey species. This situation is similar to the "alternative prey hypothesis" of Angelstam et al. (1984), which explains why certain animal species show synchronized fluctuations in Fennoscandia. Voles are known to fluctuate with a cycle of about 3 to 4 years and the dynamics of the predators (like the red fox *Vulpes vulpes*) are coupled to this prey. When the main prey declines the predators turn to alternative prey species inducing a cylce on these prey species. Our explanation implies no fluctuations in the main prey of the beech marten; we only hypothesize that an increased predator density should have an inhibiting impact on the alternative prey. This is similar to Janzen's (1976) explanation of the low reptile biomass in Africa. Janzen believes that many predators are able to maintain high population sizes because of the large herbivore biomass. The carnivores impose predation pressure on minor prey species and lower the reptile biomass (Janzen 1976; but see Kreulen 1979).

Acknowledgements

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Zusammenfassung

Populationsdynamik des Eichhörnchens in Bayern

Für fünf Gebiete Bayerns werden die Populationsschwankungen des Eichhörnchens *(Sciurus vulgaris)* dargestellt. Zwischen 1970 und 1980 war eine Abnahme der Eichhörnchen zu beobachten, seit 1980 hingegen kam es wieder zu einer leichten Zunahme. Die Abnahme ist wohl keine Folge menschlicher Eingriffe, sondern kann auf Reproduktionswellen zurückgeführt werden, die durch die Mastjahre der Fichte bedingt sind. Die Zunahme seit 1980 wird als Folge des Waldsterbens diskutiert, da die Schädigung der Nadelbäume zu einer Desynchronisation der Zapfenproduktion geführt hat. Damit stand den Eichhörnchen eine konstante Nahrungsquelle zur Verfügung.

Wetterfaktoren scheinen die Dynamik der Eichhörnchenpopulation nicht zu beeinflussen. Dagegen finden wir eine negative Korrelation zwischen Steinmarder *(Martes foina)* und Eichhörnchen.

References

Angelstam, P.; Lindström, E.; Widen, P. (1984): Role of predation in short-term fluctuations of some birds and mammals in Fennoscandia. Oecologia **62**, 199–208.

Brandl, R. (1983): Populationstrend des Eichhörnchens *Sciurus vulgaris* L. in der Oberpfalz. Säugetierkundl. Mitt. **31**, 76–78.

Formosov, A. N. (1933): The crop of cedar nuts, invasions into Europa of the Siberian nutcracker (*Nucifraga caryocatactes macrorhynchus* Brehm) and fluctuations in numbers of the squirrel (*Sciurus vulgaris* L.). J. Anim. Ecol. **2**, 70–81.

Gurnell, J. (1983): Squirrel numbers and the abundance of tree seeds. Mammal Rev. **13**, 133–148.

Möckel, R. (1987): Bemerkenswerter Massenwechsel des Eichhörnchens *(Sciurus vulgaris)* im West-Erzgebirge. Säugetierkdl. Inf. **11**, 489–493.

Janzen, D. A. (1976): The dependence of reptile biomass by large herbivores. Am. Nat. **110**, 371–400.

Kreulen, D. A. (1979): Factors affecting reptile biomass in African grasslands. Am. Nat. **114**, 157–165.

Potts, G. R.; Tapper, S. C.; Hudson, P. J. (1984): Population fluctuations in red grouse: analysis of bag records and a simulation model. J. Anim. Ecol. **53**, 21–36.

Pulliainen, E. (1973): Winter ecology of the red squirrel (*Sciurus vulgaris* L.) in northeastern Lapland. Ann. Zool. Fennici. **10**, 487–494.

Pulliainen, E. (1984): The predation system seed-squirrel-marten under subarctic conditions. Z. Säugetierkunde **49**, 121–126.

Reichholf, J. (1974): Die Auswirkungen der Fichtensamen-Rekordernte von 1971 auf die Populationen von Buntspecht und Eichhörnchen am Unteren Inn. Natur und Landschaft **49**, 77–78.

Reichholf, J. (1983): Bestandsentwicklung und Farbphasen des Eichhörnchens *Sciurus vulgaris* L. in Südbayern. Säugetierkundl. Mitt. **31**, 73–75.

Schröder, W.; Schröder, J.; Scherzinger, W. (1982). Über die Rolle der Witterung in der Populationsdynamik des Auerhuhns *(Tetrao urogallus)*. J. Orn. **123**, 287–296.

Schulze, E.-D. (1989): Air pollution and forest decline in a spruce *(Picea abies)* forest. Science **244**, 776–783.

Stubbe, H. (1988): Das Buch der Hege. Bd. 1: Haarwild. Berlin; VEB Deutscher Landwirtschaftsverlag.

Tonkin, J. M. (1983): Activity patterns of the red squirrel *(Sciurus vulgaris)*. Mammal Rev. **13**, 99–111.

Wauters, L.; Dhondt, A. (1989): Body weight, longevity and reproductive success in red squirrels *(Sciurus vulgaris)*. J. Anim. Ecol. **58**, 637–651.

Wiltafsky, H. (1978): *Sciurus vulgaris* Linnaeus, 1758 – Eichhörnchen. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer and F. Krapp. Wiesbaden: Akademische Verlagsgesellschaft. Bd. **1**, 86–105.

Zwahlen, R. (1975): Die lokomotorische Aktivität des Eichhörnchens *(Sciurus vulgaris)*. Oecologia **22**, 79–98.

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